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REVIEW

A critical evaluation of host ranges of parasitoids of the subtribe Diabroticina (Coleoptera: Chrysomelidae: Galerucinae: Luperini) using field and laboratory host records

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The subtribe Diabroticina is a large group of New World Chrysomelidae that includes corn rootworms, cucumber beetles and other pests. Recent introductions of *Diabrotica virgifera virgifera* LeConte into Europe, and the development of resistances to current management practices of rootworms in the USA have increased interest in new sustainable options for managing those pests. The only parasitoids that have been shown to consistently target and develop inside the beetle adults are *Centistes gasseni* Shaw, *Centistes diabroticae* Gahan (both Hym.: Braconidae), and *Celatoria diabroticae* Shimer, *Celatoria compressa* (Wulp), *Celatoria bosqi* Blanchard, and *Celatoria setosa* Coquillett (all Diptera: Tachinidae). This review improves our understanding of the realised and potential host range of these known parasitoids by rectifying erroneous references in light of new host records and from laboratory host range tests. Based on this critical review, all tachinid and braconid species studied are considered to be specific at least to the level of subtribe, i.e. Diabroticina. *Celatoria setosa, Celatoria diabroticae* and *C. bosqi*, have a narrow realised and potential host range; the former is restricted to the genus *Acalymma* and the last two to the *fucata* and *virgifera* groups of the genus *Diabrotica*. The braconids *Centistes gasseni* and *C. diabroticae* are also specific. The realised host range of *C. gasseni* includes species in the *Diabrotica fucata* and *virgifera* groups; while its potential host range also includes *Acalymma* species. The realised and potential host range of *Centistes diabroticae* includes *Acalymma* species as well as species in the *fucata* and *virgifera* groups of *Diabrotica*. *Celatoria compressa* has the broadest realised range compared to the other species studied, since it was obtained from species in several genera of Diabroticina; and its potential host range may also include Old World *Aulacophora* species.

Keywords: realised host range; potential host range; *Celatoria*; *Centistes*; classical biological control; ecological host range; fundamental host range

Introduction

The subtribe Diabroticina (Coleoptera: Chrysomelidae: Galerucinae: tribe Luperini) contains a large number of oligophagous and polyphagous species that feed on a wide variety of agricultural crops and ornamental and wild plants in the Americas (Jolivet and Verma 2002). Plant damage is caused by adults feeding on the foliage, fruits or flowers and

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by root-feeding larvae. In particular, the genera *Acalymma* Barber (Section Diabroticites), *Cerotoma* Chevrolat (synonym *Andrector* Horn) (Section Cerotomites), and *Diabrotica* Chevrolat (Section Diabroticites), include important agricultural pests (Anonymous 2007). *Acalymma bivittula* (Kirsch) and *A. bruchii* (Bowditch) are serious pests of cucurbits in South America, whereas in North America the genus is represented by the striped cucumber beetle, *Acalymma vittatum* (synonym *vittata*) (Fabricius). The most important pests in the genus *Cerotoma* are the bean leaf beetle *C. trifurcata* (Forster), which attacks leguminous crops throughout the eastern USA (Kogan, Waldbauer, Boiteau, and Eastman 1980), and *C. arcuata* Olivier, a pest of legumes in Brazil (Nava and Parra 2003). The genus *Diabrotica* is divided into the *virgifera,* the *fucata,* and the *signifera* group. The former two groups include important pests of row crops and vegetables (Krysan and Smith 1987). Within the *fucata* group, *Diabrotica speciosa* (Germar) is a key pest of beans, maize, cucurbits and soybeans in Argentina and Brazil, whereas in North America, *D. undecimpunctata howardi* Barber, and *D. u. undecimpunctata* Mannerheim cause serious economic losses in maize and other crops (Jolivet and Verma 2002). Within the *virgifera* group, *Diabrotica virgifera zeae* Krysan & Smith and *D. v. virgifera* LeConte devastate maize crops in North America (Krysan and Miller 1986). Furthermore, several recent introductions of *D. v. virgifera* to Europe (Miller et al. 2005), makes this beetle a growing threat (Baufeld and Enzian 2005).

Historically, various chemical and cultural methods have limited losses in maize yield (Krysan and Miller 1986; Chandler, Coppedge, Edwards, Tollefson, and Wilde 2000). However, concerns about environmental damage, insecticide resistance (Ward et al. 2005), expected resistances to genetically modified *Bt*-maize (Crowder and Onstad 2005) and prolonged diapauses or behavioural adaptations to crop rotation (Levine and Oloumi-Sadeghi 1996) have raised interests for alternative management methods for *Diabrotica* pest species. Classical biological control using parasitoids from native habitats in the area of origin (Waage 1990; van Driesche and Hoddle 2000) is a potential and highly recommended tactic against invasive alien pest populations (Wittenberg and Cock 2001), such as *D. v. virgifera* in Europe and even in parts of North America (Kuhlmann and van der Burgt 1998). The aim of classical biological control is to partially reconstruct the natural enemy complex of an alien pest (Mills 1994). On the other hand, the use of augmentative and conservation biological control could be considered to manage *Acalymma*, *Cerotoma* and *Diabrotica* pests throughout the Americas by mass-releasing or enhancing native parasitoids (Fischer 1983; Brust 1990).

Based on current knowledge, *Diabrotica* species are attacked by a range of pathogens, nematodes, predators and parasitoids in the area of origin, some of which appear to be specifically adapted for parasitising their hosts (Kuhlmann and van der Burgt 1998). While no parasitoids are known to target larvae in the subtribe Diabroticina (Javier and Peralta 1975; Kuhlmann and van der Burgt 1998), tachinids in the genus *Celatoria* Coquillett (Diptera: Tachinidae: Exoristinae: Blondeliini) (synonyms *Chaetophleps* Coquillett, *Neocelatoria* Walton) and braconids in the genus *Centistes* Haliday (Hymenoptera: Braconidae: Euphorinae: tribe Centistini) are parasitoids of *Diabrotica* adults (Shaw 1985; Cox 1994).

The host range of potential biological control agents must be known to assess whether non-target native species may be impacted by the introduction of an agent (Sands and van Driesche 2003). A parasitoid's host range can be characterised by its realised or potential host range. The realised (synonym ecological) host range comprises the current and evolving set of host species used for successful reproduction in nature (Nechols, Kauffman, and Schaefer 1992; Onstad and McManus 1996). The potential (synonym fundamental)

host range is the genetically delimited range and additionally includes species that were found to support development of a parasitoid under laboratory conditions (Onstad and McManus 1996; Haye, Kuhlmann, Goulet, and Mason 2006).

Within the last two decades, concerns about past introductions of arthropod biological control agents have increased because a lack of careful screening has resulted in the release of exotic generalist predators and parasitoids that had negative environmental impacts (Obrycki, Elliott, and Glies 2000; Henneman and Memmott 2001; Elkinton and Boettner 2004). A complete evaluation of host range should include reviews of scientific literature (De Nardo and Hopper 2004; Sands and van Driesche 2004), laboratory host range tests (Van Lenteren et al. 2003; Van Driesche and Murray 2004), and field surveys in the agent's native area (Fuester et al. 2001; Haye, Goulet, Mason, and Kuhlmann 2005).

Celatoria and *Centistes* species have been considered for classical or augmentative and conservation biological control of *Diabrotica* species in North America and particularly in Europe (Kuhlmann and van der Burgt 1998). However, the scarce literature that addresses the host ranges of such parasitoids has never been thoroughly reviewed, and is fraught with misidentifications, lack of detail, and indiscriminate citations of original findings. Some parasitoids have rarely or never been subsequently found within the host species as is supposed by previous reports. In the last decade, new host records from laboratory and field studies have been published allowing us to critically re-evaluate the knowledge on the host range of adult parasitoids of Diabroticina. Understanding current knowledge of host ranges will provide important information in subsequent field and laboratory evaluations of biological control agents for *D. v. virgifera* and other Diabroticina.

Materials and methods

Sources of parasitoid and host records

First, a list of all parasitoids recorded to parasitise beetles in the subtribe Diabroticina, most importantly in the genera *Acalymma, Amphelasma* Barber, *Diabrotica*, *Cerotoma*, *Gynandrobrotica* Jacoby, *Isotes* Wilcox, *Paratriarius* Schaeffer, and *Platybrotica* Cabrera Walsh was compiled. Major sources were (a) parasitoid catalogues listing species from the Americas (van der Wulp 1890; Coquillett 1897; Sabrosky and Arnaud 1965; Thompson and Simmonds 1965; Thompson 1968; Herting 1973; Arnaud 1978; Krombein, Hurd, Smith, and Burks 1979; Wood 1985; Cox 1994; O'Hara and Wood 2004; Thompson 2004), and (b) literature databases including the CAB Archive abstract database (Anonymous, 1913–1973), the CAB Abstracts (Anonymous, 1973–2006) and the NEBIS catalogues of Swiss libraries (Anonymous, 1800–2006), and (c) local libraries, collection catalogues and museum reports in Brazil, Argentina, and Mexico, as well as at the British Natural History Museum (BMNH) in London, UK, at the United States Natural History Museum (USNM) in Washington, USA, at the Canadian National Collection (CNC) of Insects in Ottawa, Canada, in Everardo Blanchard's private collection which is in the Museo Argentino de Ciencias Naturales (MACN) in Buenos Aires, Argentina, and finally at the University of Wyoming's Rocky Mountain Systematic Entomology Laboratory (RMSEL) in Laramie in Wyoming, USA.

Second, the list of recorded parasitoids was supplemented with information from the above sources implicating hosts, known non-hosts, and parasitoid geography as well as original parasitoid descriptions.

Third, a host list was established from laboratory-based host range tests, such as choice and no-choice tests or parasitoid injections into beetles (see Fischer 1981, 1983; Schroder

and Athanas 2002; Cabrera Walsh 2004; Kuhlmann, Toepfer, and Zhang 2005; Zhang, Toepfer, and Kuhlmann 2008).

Evaluation of host range

The evaluation of the realised and potential host ranges of parasitoids was carried out following the recommendations of Strand and Obrycki (1996), De Nardo and Hopper (2004), and Sands and van Driesche (2004):

1. The current *taxonomic status* and any past synonyms of recorded parasitoids were determined.
2. *Doubtful host records* were distinguished from reliable ones if (a) recent studies demonstrated taxonomic error in previous records and descriptions, or if (b) host records were mentioned only once without corroboration from later surveys or from laboratory host range tests and when such inconsistency was not suspected to be caused by differences in geographical biotypes (Sands and van Driesche 2004). Single records that were not excluded by this method were called *accidental hosts* in an ecological sense (U. Schaffner 2008, personal communication).
3. *Non-hosts* in the Diabroticina were determined in the case of (a) negative host records for a certain species at least twice in the literature, or (b) not finding a parasitoid from at least 100 but often many more individuals of a certain Diabroticina species while the parasitoid was simultaneously and frequently found in other Diabroticina at the same site over at least 2 years (see surveys of Eben and Barbercheck 1996; Cabrera Walsh 2003, 2004; Gámez-Virués and Eben 2005; Dequech et al. 2006); or (c) no observed attack of and no development in a species offered in laboratory host range tests.
4. The *realised host range* of the parasitoids in their area of origin was estimated using reliable positive and negative host records in a centrifugal approach starting with species and sub-species in the genus *Diabrotica*, then in genera of the subtribe Diabroticina, then in the tribe Luperini and finally in related tribes of the subfamily Galerucinae or even related subfamilies (Wapshere 1974).
5. The *potential host range* of the parasitoids was estimated by combining the results from laboratory host range tests with the parasitoids' realised host range (e.g. Fischer 1983; Schroeder and Athanas 2002; Cabrera Walsh 2004; Kuhlmann et al. 2005). In this review, host records from injections of parasitoid eggs or larvae into beetle haemocoel (Fischer 1983) are distinguished as *physiologically suitable hosts*, because these experiments exclude behavioural aspects requisite for listing in the parasitoid's potential host range (Zilahi-Balogh, Broeckling, Kok, and Salmon 2005).
6. *Main hosts* (synonym primary hosts) were determined for each parasitoid species being the host(s) most commonly associated with a parasitoid (Steiner et al. 2003) according to analyses (1) to (5).

Results

In their areas of origin in the Americas, adult Diabroticina host at least four parasitoid species in the genus *Celatoria*, and two species in the genus *Centistes* (Tables 1–3). These are the two key parasitoid genera as they are regularly found parasitising Diabroticina beetles.

In Europe, no parasitoids have been found in association with any life stage of the invasive *D. v. virgifera* (Toepfer and Kuhlmann 2004).

Celatoria bosqi *Blanchard* (*Dipt.: Tachinidae*)

The South American *Celatoria bosqi* was first described by Blanchard (1937) from *Diabrotica speciosa* (holotype in MACN). It has since been collected from only three *Diabrotica* species: mainly from *D. speciosa* in the *fucata* group, rarely from *D. viridula* (Fabricius) in the *virgifera* group, rarely from an undescribed *Diabrotica* sp.; and additionally once in a *Hystiopsis* sp. (Diabroticina: Cerotomites) (Cabrera Walsh 2004; Cabrera Walsh and Cabrera 2004) (Table 1). Next to the very abundant *D. speciosa* or *D. viridula,* over 6700 specimens of Diabroticina (94%) and other species in the subfamilies Galerucinae (2%), Alticinae (<1%), Eumolpinae (2%), and Megascelinae (<1%) were collected in comparable habitats between 1997 and 2002, but none, except the above mentioned *Diabrotica* species, were found to host *C. bosqi* (Cabrera Walsh 2004). Diabroticina non-hosts included: *Acalymma albidovittata* (Baly), *A. bivittula*, *A. bruchii*, *Diabrotica emorsitans* Baly, *D. kirbyi* Baly, *D. limitata* (Sahlberg), *Paranapiacaba duodecimmaculata* (Klug), *P. significata* (Gahan) and *Platybrotica misionensis* Cabrera and Cabrera Walsh (Cabrera Walsh 2003, unpublished data; Cabrera Walsh 2004; Dequech et al. 2006). Also, extensive collections of *Cerotoma arcuata* never yielded this parasitoid (Cabrera Walsh 2004; Dequech et al. 2006), suggesting the record from *C. arcuata* by Magalhães and Quintela 1987) is incorrect.

In laboratory host range tests, *C. bosqi* did not attack any of the members of the *virgifera* group of *Diabrotica*, whereas it parasitised and readily developed in *D. speciosa* of the *fucata* group (Cabrera Walsh 2004) (Table 4).

In conclusion, the realised and potential host range of *C. bosqi* is restricted to the genus level of *Diabrotica*, covering species in the *fucata* and rarely in the *virgifera* group (Figure 1). Its main host is *D. speciosa.*

Celatoria compressa (*Wulp*) (*Dipt.: Tachinidae*)

The Mexican species *Celatoria compressa* was originally described in the genus *Degeeria* by Wulp (1890) without host information (lectotype female in BMNH) (Wood 1985). It has since been found to parasitise species in the genera *Acalymma*, *Cerotoma*, *Gynandrobrotica* and *Diabrotica* (Table 2). The last included *D. v. virgifera*, and four other *virgifera* group species (Eben and Barbercheck 1996; Eben 2001, unpublished data) as well as five *fucata* group species (Gámez-Virués and Eben 2005). Despite extensive surveys, this parasitoid has never been reared from *Amphelasma*, *Isotes* or *Paratriarius*, or in other beetles from the subfamilies Galerucinae, Alticinae, Eumolpinae, and Megascelinae in the same habitat as the surveyed Diabroticina.

In laboratory host range tests, *C. compressa* parasitised and successfully developed in *D. v. virgifera* and *D. balteata* LeConte (Kuhlmann et al. 2005; Zhang 2004, unpublished data) (Table 5). It rarely parasitised and developed in *Aulacophora foveicollis* Lucas (Chrysomelidae: Galerucinae: Luperini; Subtribe Aulacophorina) (Kuhlmann et al. 2005), a pumpkin pest in north-west Asia and in Europe's south-eastern edge (Anonymous 2007). It never attacked or developed in six chrysomelid species outside the Diabroticina, and in the Curculionidae and Coccinellidae offered (Kuhlmann et al. 2005; Zhang et al. 2008).

In conclusion, *C. compressa*'s realised host range comprises the Diabroticina subtribe, while its potential host range is on the tribe level, including other Luperini (Figure 1). Its

Table 1. Host records of tachinid parasitoid species parasitising adult Diabroticina beetles in South America.

Parasitoid species	Diabroticina species	Parasitism	Country	Source
Celatoria bosqi Blanchard	[*Cerotoma arcuata* Olivier	1–32%	Brazil	Magalhães and Quintela (1987)]
	Diabrotica speciosa[f] (Germar)	1–28%	Argentina, Bolivia, Brazil, Paraguay, Uruguay	Blanchard (1937), Christensen (1943), Parker et al. (1951), D'A.- Silva et al. (1968), Gassen (1984, 1989), Salles (1996), Heineck-Leonel and Salles (1997), Cabrera Walsh (2004), Dequech et al. (2006)
	D. viridula (Fabricius)[v]	<0.1%	Argentina	Cabrera Walsh (2004)
	Hystiopsis sp.	extremely rare	Argentina	Cabrera Walsh (2004)
Undescribed *Celatoria* n. sp.	*D. limitata* (Sahlberg)[f]	2.5%	Argentina, Brazil	Cabrera Walsh (2001, unpubl. data)
Unidentified *Strongygaster* sp.	*C. arcuata*	extremely rare	Brazil	Micheli (2005)

[ ] Citations that are not verified by ensuing surveys or by host range tests (see Table 4). [f] *fucata* group species. [v] *virgifera* group species.

main hosts are *A. trivittata* (Mannerheim), *A. innubum* (Fabricius), *D. scutellata* Baly, *D. tibialis* Jacoby, *D. porracea* Harold and *D. v. virgifera*.

Celatoria diabroticae (*Shimer*) (*Dipt.: Tachinidae*)

The North American *Celatoria diabroticae* was originally described in the genus Tachina by Shimer in 1871 (type material missing) (Wood 1985). In the USA, both *D. undecimpunctata howardi* (Summers and Stafford 1953; Fischer 1981), and *D. u. undecimpunctata* (Fischer 1983) experience high parasitism rates by *C. diabroticae* (Table 2). *Celatoria diabroticae* is found less often in *Diabrotica longicornis* (Say) (Fischer 1983) or *D. barberi* (Prischmann and Dashiell 2008) and rarely in *D. v. virgifera* (Fischer 1981, 1983). Reports of parasitism in species of the genus *Acalymma*, such as *A. trivittata* (Shimer 1871; Arnaud 1978) and *A. vittata* (Bussart 1937; Fattig 1949; Arnaud 1978), were never confirmed in later surveys. Furthermore, no *Acalymma* species were attacked in laboratory host range tests (Fischer 1983). McConnell (1915) claimed to have reared *C. diabroticae* from *Cerotoma trifurcata*; however, it is not clear from the report how he recognised this species (Fischer 1983). Subsequent papers by Eddy and Nettles (1930), Isely (1930), Fronk (1950), Herzog (1977), Arnaud (1978), and Marrone, Brooks, and Stinner (1983) relied upon the parasitoid identification of McConnell (1915). Since *C. diabroticae* never attacked *C. trifurcata* in laboratory host range tests, it seems likely that McConnell's report was based on a misidentification of the parasitoid (Fischer 1983). To date, it remains unknown which *Celatoria* species is found on *Cerotoma trifurcata* in the USA (Danielson, Brandle, and

Table 2. Host records of tachinid parasitoid species parasitising adult Diabroticina beetles in North America.

Parasitoid species	Diabroticina species	Parasitism	Country	Source
Celatoria compressa (Wulp)	*Acalymma blomorum* Munroe and Smith	1–3.7%	Mexico	Eben and Barbercheck (1996), Gámez and Eben (2005)
	A. fairmairei (Fabricius)	0.4–3%	Mexico	Eben and Barbercheck (1996), Gámez and Eben (2005)
	A. innubum (Fabricius)	0.8–8%	Mexico	Eben and Barbercheck (1996), Gámez and Eben (2005)
	A. trivittata (Mannerheim)	8%	Mexico	Eben and Barbercheck (1996)
	Cerotoma atrofasciata Jacoby	2–12.5%	Mexico	Gámez and Eben (2005)
	Diabrotica balteata LeConte[f]	3–10%	Mexico	Gámez and Eben (2005)
	D. porracea Harold[v]	0.5–7.5%	Mexico	Eben and Barbercheck (1996), Gámez and Eben (2005)
	D. scutellata Baly[v]	1.4–10%	Mexico	Eben and Barbercheck (1996), Gámez and Eben (2005)
	D. sexmaculata Baly[f]	5%	Mexico	Gámez and Eben (2005)
	D. tibialis Jacoby[f]	4–11%	Mexico	Eben and Barbercheck (1996), Gámez and Eben (2005)
	D. viridula (Fabricius)[v]	0.5–7.5%	Mexico	Eben and Barbercheck (1996)
	D. v. virgifera LeConte[v]	6.6–16%	Mexico	Eben and Alvarez (2001, unpubl. data)
	D. v. zeae Krysan and Smith[v]	rarely	Mexico	Eben and Alvarez (2001, unpubl. data)
	Gynandrobrotica lepida (Say)	<0.1%	Mexico	Eben (2002, unpubl. data)
	G. nigrofasciata (Say)	2.5%	Mexico	Gámez and Eben (2005)
Celatoria diabroticae (Shimer)	*A. trivittata*	rarely	USA	Essig (1926), Arnaud (1978)
	A. vittatum (= *vittata*) (Fabricius)	rarely	USA	Walton (1914), Chittenden (1919), Bussart (1937), Lowry (1918), Fattig (1949), Arnaud (1978)
	C. trifurcata (Foerster)	1–20%	USA	McConnell (1915), Eddy and Nettles (1930), Isely (1930), Fronk (1950), Herzog (1977), Marrone (1983)
	D. barberi Smith Lawrence	<1%	USA	Prischmann and Dashiell (2008)
	D. longicornis (Say)[v]	3%	USA	Fischer (1983)
	D. u. howardi Barber[f]	2–35%	USA	Sell (1915), Fronk (1950), Summers and Stafford (1953), Arnaud (1978), Fischer (1983), Gordon et al. (1987), Meinke and Gould (1987), Elsey (1988), Luginbill (1940), Isely (1930), Sweetman (1926), Arant (1929), Weber (2006, unpubl. data)

Table 2 (*Continued*)

Parasitoid species	Diabroticina species	Parasitism	Country	Source
	D. u. undecimpunctata Mannerheim[f]	1–35%	USA	Michelbacher et al. (1943), (1955), Rookwood and Chamberlin (1943), Arnaud (1978), Fischer (1981)
	D. v. virgifera[v]	<1%	USA	Fischer (1983)
	[*Trirhabda bacharidis* (Weber)**	unknown	USA	Johnson (1925)]
Celatoria setosa (Coquillett)	*A. blandula* LeConte	unknown	USA	Fischer (1983)
	A. trivittata	unknown	Mexico	Fischer (1983), Alvarez and Toepfer (2002, unpubl. data)
	A. vittatum (=*vittata*)	4–44%	USA	Chittenden (1919), Bussart (1937), Gould (1944), Arnaud (1978), Fischer (1981), Elsey (1988), Smyth (1999, unpubl. Data)
	[*D. u. howardi*[f]	rarely	USA	Fattig (1949), Fischer (1981)]
	[*D. u. undecimpunctata*[f]	rarely	USA	Bussart (1937), Fischer (1981)]
Celatoria maracasi Thompson	unknown	unknown	Trinidad	Thompson (1968)
Undescribed *Celatoria* n. sp.	*C. trifurcata*	<1%	USA	Danielson et al. (2000)
Undescribed *Medina* sp. (near *quinteri* (Townsend)*	*C. trifurcata*	up to 40%	USA	Loughran and Ragsdale (1986)*
Strongygaster (orig. in *Hyalomyodes*) *triangulifer* (Loew)	*C. trifurcata*	rarely	USA	Herzog (1977), Marrone (1983)
Myiopharus (orig. in *Pseudomyothyria*) *ancillus* Walker	[*D. u. undecimpunctata*[f]	rarely	USA	Brauer and Bergenstamm (1895), Arnaud (1978)]

[ ] Citations that are not verified by ensuing surveys or by host range tests (see Table 5). * Possibly similar to the undescribed *Celatoria* n. sp. of Danielson (2000). ** *Trirhabda bacharidis* does not belong to the subtribe Diabroticina within the Luperini, but to Galerucini. This single record was never verified by ensuing surveys. [f] *fucata* group species. [v] *virgifera* group species.

Hodges 2000). It is suspected to be the same as the *Medina* sp. found in *C. trifurcata* by Loughran and Ragsdale (1986) (see below). Finally, a single record on a Galerucinae beetle in the tribe Galerucini, i.e. on *Trirhabda bacharidis* (Weber), by Johnson (1925), is anomalously distant from the rest of the known hosts and was never reported again. It is likely to be an error and would need confirmation before it could be accepted (Sands and van Driesche 2004).

In laboratory host range tests, *C. diabroticae* parasitized *Diabrotica* species of both the *fucata* and *virgifera* groups (Fischer 1983). Although *C. diabroticae* did not parasitise *Acalymma* or *Cerotoma* species, its larvae were able to develop when injected inside hosts in both genera (Fischer 1983). *Acalymma* and *Cerotoma* are thus physiologically suitable hosts outside its potential host range. No development of the parasitoid larvae was observed in *Coccinella septempunctata* L. (Coccinellidae) (Fischer 1983).

Table 3. Host records of braconid parasitoid species parasitising adult Diabroticina beetles in the Americas.

Parasitoid species	Diabroticina species	Parasitism	Country	Source
Centistes diabroticae (Gahan)	*Acalymma vittatum* (=*vittata*) (Fabricius)	0–23%	USA	Gahan (1922), Krombein (1979), Fischer (1981), Smyth (1999, unpubl. data)
	Diabrotica balteata LeConte[f]	0–4%	Mexico	Hiltpold and Toepfer (2006, unpubl. data)
	D. v. zeae Krysan and Smith[v]	0–8%	Mexico	Hiltpold and Toepfer (2006, unpubl. data)
Centistes gasseni Shaw	*A. bivittula* (Kirsch)	extremely rare	Brazil	Cabrera Walsh et al. (2003)
	D. speciosa (Germar)[f]	0.5–18%	Argentina, Brazil, Paraguay	Heineck-Leonel and Salles (1997), Schroder and Athanas (2002), Cabrera Walsh (2003) Cabrera Walsh et al. (2003)
	D. viridula (Fabricius)[v]	0.2–11%	Argentina, Brazil, Paraguay	Cabrera Walsh et al. (2003)
	D. limitata (Sahlberg)[f]	7.5%	Argentina, Brazil	Cabrera Walsh et al. (2003)

[f] *fucata* group species. [v] *virgifera* group species

In conclusion, *Celatoria diabroticae* has a realised and potential host range on the genus level, encompassing species in the *fucata* and *virgifera* groups of *Diabrotica* (Figure 1). Its main hosts are the *fucata* group species *D. u. howardi* and *D. u. undecimpunctata*.

Celatoria setosa (*Coquillett*) (*Dipt.: Tachinidae*)

This North American species was originally described by Coquillett (1890, 1895b) as *Chaetophleps setosa* from Maryland, USA (lectotype male in USNM). It was then re-described by Walton (1914) as *Neocelatoria ferox* (holotype female in USNM, Washington,

Table 4. Laboratory host range tests with tachinid parasitoid species parasitising adult Diabroticina beetles in South America.

Parasitoid species	Beetle species	Attack	Development	Source
Celatoria bosqi Blanchard	*Diabrotica calchaqui* Cabrera Walsh[v]	No	–	Cabrera Walsh (2004)
	D. v. virgifera LeConte[v]	No	–	Zhang (2001, unpubl. data)
	D. viridula (Fabricius)[v]	No	–	Cabrera Walsh (2004)
	D. speciosa (Germar)[f]	Yes	Yes	Cabrera Walsh (2004)

[f] *fucata* group species. [v] *virgifera* group species.

USA) (Wood 1985). Field records in the USA and Mexico as well as data from laboratory host range tests indicate that *C. setosa* is restricted to *Acalymma* species including *A. blandula* LeConte, *A. trivittata* and *A. vittatum* (Bussart 1937; Arnaud 1978; Fischer 1983; Elsey 1988a,b) (Tables 2 and 5). In rare cases in the USA, *C. setosa* has been reported to parasitize *D. u. undecimpunctata* and *D. u. howardi* (Bussart 1937; Arnaud 1978; Elsey 1988b). No additional records were produced in *D. u. undecimpunctata, D. u. howardi* or *D. longicornis* from extensive field surveys by Fischer (1983), and laboratory host range testing suggests these are not within the potential host range of *C. setosa* (Fischer 1983). In the laboratory, the parasitoid attacked and developed readily in several *Acalymma* species, but completely ignored other genera (Fischer 1983). Likewise, injected larvae only developed in *Acalymma* (Fischer 1983) (Table 5).

Consequently, the realised and potential host ranges of *C. setosa* are restricted to *Acalymma* species (Figure 1), with *A. vittatum* as the parasitoid's main host.

Centistes diabroticae (*Gahan*) (*Hym.: Braconidae*)

This North American braconid in the Euphorinae tribe Centistini was originally described as *Syrrhizius diabroticae* by Gahan (1922) (holotype in USNM). It has since been collected from *A. vittatum* in the USA (Gahan 1922; Krombein et al. 1979; Fischer 1981) as well as from *D. v. zeae* and *D. balteata* in Mexico (Hiltpold and Toepfer 2006, unpublished data).

Consequently, this parasitoid is suggested to have a realised host range on section level, covering Diabroticites including: species in the *fucata* and *virgifera* groups of *Diabrotica* as well as *Acalymma* species (Figure 1), with *A. vittatum* as its main host. The host range of *C. diabroticae* under laboratory conditions remains largely untested.

Centistes gasseni *Shaw* (*Hym.: Braconidae*)

The South American *C. gasseni* was originally described by Shaw (1995) from *D. speciosa* (holotype in RMSEL). It parasitises adults of three *Diabrotica* species in northeastern Argentina, eastern Paraguay and southern Brazil (Table 3): *D. speciosa*, and *D. limitata* in the *fucata* group, and *D. viridula* in the *virgifera* group. *Acalymma bivittula* is considered an accidental host from a single record of *C. gasseni* emergence out of 3960 beetles collected in the parasitoid's geographical range between 1997 and 2002 (Cabrera Walsh, Athanas, Salles, and Schroder 2003). In the same period and next to about 100,000 *D. speciosa*, *D. limitata* or *D. viridula*, over 6700 specimens of species in different Diabroticina genera (94%) and of other species in the subfamilies Galerucinae (2%), Alticinae (<1%), Eumolpinae (2%), and Megascelinae (<1%) were collected in comparable habitats, but none, except the above-mentioned, were found to host *C. gasseni* (Cabrera Walsh 2003; Cabrera Walsh et al. 2003). These negative hosts included such Diabroticina as *Acalymma albidovittata* (Baly), *A. bruchii* (Bowditch), *Cerotoma arcuata*, *Diabrotica emorsitans*, *D. kirbyi*, *Paranapiacaba duodecimmaculata*, *P. significata* and *Platybrotica misionensis* (Cabrera Walsh et al. 2003; Cabrera Walsh and Cabrera 2004). A hyperparasitoid, *Mesochorus* sp. (Hymenoptera: Ichneumonidae), was reported from *C. gasseni* cocoons in Argentina (Cabrera Walsh et al. 2003).

In laboratory host range tests, *C. gasseni* parasitised and developed readily in three North American *Diabrotica* species and in *A. vittatum* (Table 6). *Centistes gasseni* rejected *Cerotoma trifurcata* (Foerster), and the eight Coccinellidae species offered (Schroder and Athanas 2002).

Table 5. Laboratory host range tests with tachinid parasitoid species parasitising adult Diabroticina beetles in North America.

Parasitoid species	Beetle species	Attack	Development	Source
Celatoria compressa (Wulp)	*Diabrotica balteata* LeConte[f]	Yes	Yes	Zhang (unpubl. data)
	D. v. virgifera LeConte[v]*	Yes	Yes	Kuhlmann et al. (2005)
	Adalia bipunctata L. (Coccinellidae)	No	–	Kuhlmann et al. (2005)
	Aulacophora foveicollis Lucas (Chrysomelidae: Galerucinae)	Yes	Rarely	Kuhlmann et al. (2005)
	Cassida rubiginosa Mueller (Chrysomelidae: Cassidae)	No	–	Kuhlmann et al. (2005)
	Galerucella pusilla Duftschmidt (Chrysomelidae: Galerucinae)	No	–	Kuhlmann et al. (2005)
	Gastrophysa viridula Deg. (Chrysomelidae: Chrysomelinae)	No	–	Kuhlmann et al. (2005)
	Gonioctena furnicata Brüggem. (Chrysomelidae: Chrysomelinae)	No	–	Kuhlmann et al. (2005)
	Pyrrhalta luteola (Mueller) (Chrysomelidae: Galerucinae)	No	–	Kuhlmann et al. (2005)
	Sitona lineatus L. (Curculionidae)	No	–	Kuhlmann et al. (2005)
Celatoria diabroticae (Shimer)	*Acalymma blandula* LeConte	No	Yes**	Fischer (1983)
	A. trivittata (Mannerheim)	No	Yes**	Fischer (1983)
	A. vittatum (=*vittata*) (Fabricius).	No	Yes**	Fischer (1983)
	Cerotoma trifurcata (Fabricius)	No	Yes**	Fischer (1983)
	Diabrotica balteata[f]	No	Yes**	Fischer (1983)
		Yes	Rarely	Weber, Kurtz and Toepfer (2006, unpubl. data)
	D. cristata (Harris)[v]	No	Yes**	Fischer (1983)
	D. longicornis (Say)[v]	Yes	Yes**	Fischer (1983)
	D. u. howardi Barber[f]	Yes	Yes**	Fischer (1983)
	D. u. undecimpunctata Mannerheim[f]	Yes	Yes**	Fischer (1983)
	D. v. virgifera[v]	Yes	Yes**	Fischer (1983)
	Coccinella septempunctata L. (Coccinellidae)	–	No**	Fischer (1983)
Celatoria setosa (Coquillett)	*A. blandula*	Yes	Yes**	Fischer (1983)
	A. trivittata	Yes	Yes**	Fischer (1983)
	A. vittatum (=*vittata*)	Yes	Yes**	Fischer (1983)
	C. trifurcata	No	No**	Fischer (1983)
	D. balteata[f]	No	No**	Fischer (1983)
	D. cristata[v]	No	No**	Fischer (1983)
	D. longicornis[v]	No	No**	Fischer (1983)

Table 5 (*Continued*)

Parasitoid species	Beetle species	Attack	Development	Source
	D. u. howardi[f]	No	No**	Fischer (1983)
	D. u. undecimpunctata[f]	No	No**	Fischer (1983)
	D. v. virgifera[v]	No	No**	Fischer (1983)
	Coccinella septempunctata L. (Coccinellidae)	No	No**	Fischer (1983)

*Central European and USA strain. **Tachinid larvae were injected into beetle body. [f] *fucata* group species. [v] *virgifera* group species.

In conclusion, this parasitoid has a realised host range on genus level, comprising *Diabrotica* species in both the *fucata* and *virgifera* groups (Figure 1), with *D. speciosa* as the main host. Its potential host range includes *Acalymma* species as well.

Other species

Celatoria maracasi Thompson (Diptera: Tachinidae) was described from the Maracas Valley in Trinidad (holotype female in CNC) (Wood 1985). Its host range and habitat are unknown (Thompson 1968).

Medina sp. (near *quinteri* (Townsend)) (Diptera: Tachinidae) was found to parasitise up to 40% of *C. trifurcata* in Minnesota, USA (Loughran and Ragsdale 1986; D.H. Wood 2007, personal communication). It has four generations per year and overwinters as larvae in its beetle hosts. Although the taxonomic status of *Medina* sp. is uncertain, it may be the parasitoid identified as *Celatoria* in *C. trifurcata* (Fischer 1983; Danielson et al. 2000), or may explain the uncertain above-mentioned records of *Celatoria diabroticae* (Table 2).

The polyphagous *Strongygaster* (originally in *Hyalomyodes*) *triangulifer* (Loew) (Diptera: Tachinidae) parasitised *C. trifurcata* in extremely low numbers (Herzog 1977; O'Hara and Wood 2004) (Table 2). This parasitoid is clearly not a key natural enemy of Diabroticina, and not worth considering as a biological control agent.

Likewise, *Myiopharus* (originally in *Pseudomyothyria*) *ancillus* (Walker) (Diptera: Tachinidae), cited to parasitise *D. u. undecimpunctata*, was never found again in a Diabroticina species (Brauer and Bergenstamm 1895; Arnaud 1978) and misidentification is likely (J. O'Hara 2007, personal communication). *Myiopharus ancillus* is better known as a parasitoid of Pyralidae and Scarabaeidae.

Occasionally, dipteran Phoridae become facultative parasitoids in crowded laboratory cultures (R.H.L. Disney 2005, personal communication). *Megaselia scalaris* (Loew) (Diptera: Phoridae) emerged from adult *D. v. virgifera* (R. Alvarez and J. Miall 2005, personal communication), and *Phalacrotophora* sp. (near *P. nedae* (Mall.)) and *P. epeirae* emerged from pupae and larvae of *D. balteata* (Saba 1970). However, these Phoridae are primarily polyphagous saprophagous species, and not candidates for the control of Diabroticina.

Discussion

Two hymenopteran braconid species and four dipteran tachinid species have been consistently observed to develop in Diabroticina adults, respectively: *Centistes gasseni* and *C. diabroticae*, *Celatoria diabroticae*, *C. compressa*, *C. bosqi*, and *C. setosa*. This list is astonishingly short considering that there are over 500 described beetle species in the subtribe Diabroticina in different habitats and geographical regions of the New World (Hsiao 1994; Jolivet and Verma 2002). High altitude sites in north-eastern South America remain unexplored, and natural enemy surveys there may yet reveal more parasitoids species. Nevertheless, the overall paucity of parasitoid community in adult Diabroticina may reflect the effectiveness of Diabroticina defence mechanisms such as (a) strong protective elytra (Jolivet and Verma 2002) and/or (b) acquisition of bitter or toxic secondary compounds such as the cucurbitacins sequestered by cucurbit-feeding beetles (Ferguson and Metcalf 1985; Eben and Barbercheck 1996).

Moreover, the results of this review strongly suggest that the genus *Celatoria* needs revision. Several types of these species appear to be lost, and the existence of some host records is in doubt. With the exception of *C. setosa, Celatoria* congeners are

Parasitoid species	Potential host range: Realised host range	Potential host range: Laboratory assessed host range
Celatoria setosa	*Acalymma*	*Acalymma*
Celatoria bosqi	*Diabrotica fucata + virgifera group*	*Diabrotica fucata group*
Celatoria diabroticae	*Diabrotica fucata + virgifera group*	*Diabrotica fucata + virgifera group* *
Centistes gasseni	*Diabrotica fucata + virgifera group, Acalymma*	*Diabrotica fucata + virgifera group, Acalymma*
Centistes diabroticae	*Diabrotica fucata + virgifera group, Acalymma*	*at least: Diabrotica virgifera group* **
Celatoria compressa	*Diabrotica fucata + virgifera group, Acalymma, Cerotoma, Gynandrobrotica*	*at least: Diabrotica fucata + virgifera group, Aulacophora,* ***

* Physiologically suitable hosts are also *Acalymma* and *Cerotoma* spp.
** There were no host range tests with the *Diabrotica fucata* group, *Acalymma*, *Cerotoma*, and *Gynandrobrotica* spp.
*** There were no host range tests with *Acalymma, Cerotoma,* and *Gynandrobrotica* spp.

Figure 1. Proposed realised (=ecological) and potential (=fundamental) host range of parasitoids of Diabroticina on the basis of host records from field surveys in their original distribution areas, as well as of results from host range tests in laboratory.

Table 6. Laboratory host range tests with braconid parasitoid species parasitising adult Diabroticina beetles in the Americas.

Parasitoid species	Beetle species	Attack	Development	Source
Centistes diabroticae (Gahan)	*Diabrotica v. virgifera*	Yes	Yes	Hiltpold, Kurtz and Toepfer (2006, unpubl. data)
Centistes gasseni Shaw	*Acalymma vittatum*	Yes	Yes	Schroder and Athanas (2002)
	Cerotoma trifurcata	No	No	Schroder and Athanas (2002)
	D. balteata[f]	Yes	Yes	Schroder and Athanas (2002)
	D. u. howardi[f]	Yes	Yes	Schroder and Athanas (2002)
	D. v. virgifera[v]	Yes	Yes	Schroder and Athanas (2002)
	Coleomegilla maculata (DeGeer) (Coccinellidae)	No	No	Schroder and Athanas (2002)
	Chilocorus stigma (Say) (Cocc.)	No	No	Schroder and Athanas (2002)
	Cycloneda munda (Say) (Cocc.)	No	No	Schroder and Athanas (2002)
	Epilachna varivestis Mulsant (Cocc.)	No	No	Schroder and Athanas (2002)
	Harmonia axyridis (Pallas) (Cocc.)	No	No	Schroder and Athanas (2002)
	Hippodamia convergens Guerin (Cocc.)	No	No	Schroder and Athanas (2002)
	Hippodamia variegata (Goeze) (Cocc.)	No	No	Schroder and Athanas (2002)

[f] *fucata* group species. [v] *virgifera* group species.

morphologically very similar, and the morphological characters used to distinguish them are feeble (N. Wyatt 2001, personal communication). The *Celatoria* species reported from *Cerotoma trifurcata* by Danielson et al. (2000), in *C. arcuata* by Magalhães and Quintela (1987), and in *Diabrotica limitata* (Cabrera Walsh 2003, unpublished data), may well be new species. Moreover the identifications of *Celatoria diabroticae* obtained from *C. trifurcata* (Eddy and Nettles 1930; Isely 1930; Fronk 1950; Herzog 1977; Marron 1983; all based on McConnell 1915) need substantiation. The South American species *Celatoria brasiliensis* Townsend (1928) has but a brief, incomplete description, devoid of illustrations and of references to hosts or habitats (Townsend 1928; Thompson 2004). *Celatoria spinosa* Coquillett (1897), a parasitoid of Alticinae, is not related to *Celatoria* species and was moved into the genus *Medina* by Wood (1985) (see also O'Hara and Wood 2004; Thompson 2004). It is also unclear if the Mexican *Celatoria* (originally in *Degeeria*) *nigricans* (Wulp) (Wulp 1890) (holotype male in BNHM) is distinct from *C. compressa* (lectotype female at BNHM) (N. Wyatt 2001, personal communication). *Celatoria crawii* Coquillett (lectotype female in USNM) served to define the genus *Celatoria* Coquillett

(1890, 1895a) (Craw 1891), but became a synonym of *Celatoria diabroticae* which had been described by Coquillett in the genus Tachina (1897) (Wood 1985; O'Hara and Wood 2004). Since the syntypes of *diabroticae* seem to be lost, revisers of *Celatoria* may designate the lectotype of *crawii* as the neotype of *diabroticae*, thereby making the two names objective synonyms (O'Hara 2007, personal communication).

Despite the taxonomic confusion and the paucity of parasitoid records, we were able to evaluate the host ranges for common parasitoids of Diabroticina beetles. The tachinid and braconid parasitoids appeared to be specific at least to the level of subtribe, which was expected for braconids that are often reported to be host specific (Godfrey 1994), but not for tachinids that were considered generalists (Herting 1994). However, this view is currently changing as more and more specialist tachinids are found among closely related generalist species or genera (Smith, Wood, Janzen, Hallwachs, and Nebert 2007).

In this review, we determined that the tachinids *C. setosa, C. bosqi* and *C. diabroticae* have narrow realised host ranges; the former is restricted to the genus *Acalymma* and the last two to the *fucata* and *virgifera* groups of *Diabrotica*. *Celatoria diabroticae* is also capable of developing in *Cerotoma* and *Acalymma* species upon injection. The braconids *C. gasseni* and *C. diabroticae* are also specific (Figure 1). The realised host range of *Centistes gasseni* includes species in the *Diabrotica fucata* and *virgifera* groups; while its potential host range also includes *Acalymma* species. Notably, the potential host range of a parasitoid is often greater than its realised host range (Cameron and Walker 1997; Morehead and Feener 2000); an artifact of laboratory settings, where the factors that influence host searching and assessment behaviour of a parasitoid in its natural environment are removed (Nechols et al. 1992; Sands 1993). The realised host range of *Centistes diabroticae* includes *Acalymma* species as well as species in the *Diabrotica fucata* and *virgifera* groups. *Celatoria compressa* has the broadest realised range compared to the other species studied above, since it was obtained from species in several genera of Diabroticina, including *Acalymma*, *Cerotoma*, *Diabrotica*, *Gynandrobrotica*, and since it showed a certain potential to parasitise the Old World genus *Aulacophora* in the laboratory.

In conclusion, *Celatoria diabroticae, C. compressa*, *Centistes diabroticae* and *C. gasseni* could be considered as possible candidates for classical biological control of *D. v. virgifera* in Europe. In North America, classical biological control with *C. bosqi* or *C. gasseni* could complement augmentative and conservation biological control of Diabroticina beetles using the species *C. compressa*, *C. setosa*, *Celatoria diabroticae* and *Centistes diabroticae*. In particular, *C. bosqi* could be considered in a biological control programme against *fucata* group *Diabrotica*, and *C. setosa* against cucumber beetles in the *Acalymma* genus. We hope that timely research will show that the use of these natural enemies will help to alleviate the threat of *D. v. virgifera* in Europe and the economic losses resulting from resistance to current managements of the Diabroticina beetles in North America.

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